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HOST BREADTH AND VOLTINISM IN GALL-INDUCING LEPIDOPTERA

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ABSTRACT. Because of specialized life systems and host relations, gall-inducing insects are believed to have narrower host breadth and lesser voltinism than other endophagous insects. These expectations were tested here using a sample of 136 species of British Lepidoptera consisting of 29 gallers in 11 families and 107 taxonomically matched endophagous nongaller controls. Gallers and nongallers were compared using biological data assembled and published by A. M. Emmet. Host breadth, scored as number of host genera, averaged 1.21 for the gallers, and 1.48 for the nongallers, and the difference is statistically significant, thus confirming host breadth expectation for this sample of Lepidoptera. This difference was generated mostly among Gelechiidae, Nepticulidae, Tortricidae, and Sesiidae. Voltinism, scored as number of generations developing per year, did not differ between gallers and nongallers. This outcome does not necessarily refute the hypothesis underlying the expectation. The cool British climate may inhibit multivoltinism, and thereby minimize differences in voltinism between gallers and nongallers.

Additional key words: Gelechiidae, Nepticulidae, Tortricidae, Sesiidae, Britain.

Galls induced by Lepidoptera vary from simple swellings to fruitlike bodies that bear little resemblance to supporting host parts. The galls are organ specific, most developing on host stems, but some developing on host reproductive structures, leaves, and roots. With few exceptions, larvae rather than ovipositing adults induce the galls. Worldwide, 352 morphospecies of gall-inducing Lepidoptera are known, of which 179 have been identified to genera and species in 20 families (Miller 2004). Greater numbers and taxonomic diversity of lepidopteran gallers are anticipated as tropical areas are explored.

Gall-inducing insects, including Lepidoptera, are believed to have narrower host breadth and to develop fewer annual generations than other endophagous insects (Cornell 1990, Raman 1994, Miller 2004). Narrow host breadth is expected because evolutionary adjustments between gall inducer and host foster foodplant specialization, a corollary of the reputed host specificity of gall inducers (Mani 1964, Shorthouse & Rohfritsch 1992, Harris & Shorthouse 1996). Lesser voltinism is expected because gall inducers seem to synchronize their phenology with that of their hosts, which would ensure that larvae have access to reactive tissues necessary for gall development, as during rapid plant growth in spring. Physiological mechanisms that might mediate this synchrony have not been investigated. These host breadth and voltinism expectations for lepidopteran gall inducers would acquire added strength if empirical tests confirmed them.

Cornell (1990) compared voltinism and other life history traits between gall inducers and leaf miners. His voltinism sample consisted of 28 species–12 leaf miners, mostly lepidopteran, and 16 gall inducers, mostly dipteran and hymenopteran. He found that voltinism averaged 1.4 generations/yr for the gall inducers and 2.5 generations/yr for the leaf miners, which is consistent with the expectation of lesser voltinism among gall inducers. In contrast to voltinism, host breadth of gall inducers in one or any combination of insect orders does not seem to have been compared empirically with that of endophagous nongallers.

Reported here are comparisons of host breadth and voltinism between gallers and nongallers in a large sample of Lepidoptera, an order poorly represented in previous cecidological studies (Miller 2004). The source of the data analyzed is Emmet's (1991) extensive life history tabulation for more than 2400 species of British Lepidoptera, the most extensively known lepidopteran fauna in the world.

MATERIALS AND METHODS

To test the hypotheses that gall-inducing Lepidoptera have narrower host breadth and lesser voltinism than other endophagous Lepidoptera, I assembled a study sample of 29 gallers and 107 endophagous nongaller controls, 136 species in all. All known British gallers were included, as listed by Spooner and Bowdrey (1995), with emendations as follows: *Argyresthia retinella* Zeller, unaccountably absent from the list, was added (Robbins 1992), and *Paranthrene tabaniformis rhinglaeforme* (Hübner), now considered synonymous with *P. tabaniformis* (Rottemburg), was removed (Špatenka et al. 1999).

The 107 endophagous nongallers were those marked in Emmet's (1991) tabulation exclusively with *b* for borer or *m* for miner, and, for *Heliozela* only, also with *c* for casebearer to match the casebearing *Heliozela* gallers. Taxonomic matching was possible at the generic level for gallers in 10 genera, and at the subfamily level for gallers in six genera, in line with principles of the comparative method (Harvey & Pagel 1991). For example, matches for the two *Ectoedemia* (Nepticulidae) gallers consisted of the 15 nongalling endophagous *Ectoedemia*, and the match for the galler *Adaina microdactyla* (Hübner) (Pterophoridae, Platyptiliinae), which has no British congeners, was *Leioptilus carphodactyla* (Hübner), the only other endophagous British member of the subfamily Platyptili-

TABLE 1. Host breadth and voltinism of British gall-inducing Lepidoptera and taxonomically matched endophagous nongallers. Data from Emmet (1991) except where noted otherwise. Family sequence follows Kristensen (1999).

Family	Species as numbered in Emmet's tabulation	N	Mean scores: Host breadth	Mean scores: Voltinism
Nepticulidae				
Gallers	23, 24	2	1.00	1.00
Nongallers	25–32, 34–39, 41	15	1.27	1.00
Heliozelidae				
Gallers	154, 157	2	1.00	1.00
Nongaller	156	1	1.00	1.00
Incurvariidae				
Gallers	138, 139	2	1.00	1.00
Nongallers	133, 136	2	1.00	1.00
Yponomeutidae				
Gallers	411, 415	2	1.50	1.00
Nongallers	401, 404, 405, 407, 410, 412, 418, 420, 422	9	1.33	1.00
Elachistidae				
Galler	906	1	1.00	1.00
Nongaller	905	1	1.00	1.00
Coleophoridae				
Gallers	486, 889, 891, 892, 893a[1]	5	1.00	1.25
Nongallers	487, 880–884, 887, 888, 890	9	1.00	1.33
Gelechiidae				
Gallers	728, 755	2	1.00	1.00
Nongallers	723–727, 727a, 729, 730, 735, 737, 744, 744a, 746–748, 753, 757, 808, 811–813, 816, 817, 821, 822, 823a, 825	27	1.71	1.33
Sesiidae				
Gallers	372, 377, 380	3	1.33	0.67
Nongallers	373–379, 381	8	1.50	0.75
Tortricidae				
Gallers	966, 1137, 1167, 1190, 1195, 1256, 1258, 1266	8	1.37	1.06
Nongallers	962, 964, 965, 967, 1168, 1192, 1194, 1196, 1197, 1199, 1200, 1200a, 1201, 1202, 1240, 1242, 1243, 1245–1247, 1249, 1253–1255, 1257, 1259–1261, 1264, 1265, 1267, 1268–1270	34	1.56	1.06
Pterophoridae				
Galler	1517	1	1.00	2.00
Nongaller	1519	1	2.00	2.00
Crambidae				
Galler	1359	1	2.00	1.00
Nongallers	1375	1	1.00	2.00
Summary				
Gallers		29	1.21	1.07
Nongallers		107	1.48*	1.11

[1] *Mompha bradleyi* Riedl, whose discovery in Britain (Harper 1994) postdates Emmet (1991).
* Mann-Whitney $U_{134df} = 1280.0$, $p_{one\ tailed} < 0.05$.

inae. Nongallers outnumber gallers in the study because plausible matches were often more numerous than the gallers matched, all being included to avoid selection bias.

Host breadth and voltinism data were extracted for both the gallers and nongallers from Emmet's (1991) tabulation. Data for one galler subsequently discovered in Britain, *Mompha bradleyi* Riedl, was obtained from Harper (1994). Host breadth was scored as number of recorded host genera. This is a stringent measure in that no distinction was made between one and more than one host species in the same genus; however, the problem of appropriately scaling and integrating genus and species scoring was thereby avoided. Scoring by species alone could not be done because the source did not consistently list numbers of host species within genera. Voltinism was scored as number of annual generations, with the case of less than one annual generation (one generation every two years) being scored as 0.5. This case had minimal impact because it occurred in only 3 of the 29 gallers (2 sesiids and 1 tortricid) and 4 of the 107 nongallers (all sesiids).

KRISTENSEN, N. P. (ED.). 1999. Lepidoptera, moths and butterflies. Evolution, systematics, and biogeography. Handbook of Zoology. Vol. 1. De Gruyter, New York.
LEWIS, H. A. G. 1994. The Times atlas of the world. 9th ed. Times Books, London.
MANI, M. S. 1964. Ecology of plant galls. Dr Walter Junk, The Hague, The Netherlands.
MCEVOY, P. B. 1996. Host specificity and biological control. BioSci. 46:401–405.
MILLER, W. E. 2004. Gall-inducing Lepidoptera, pp. 429–462. *In* Raman, A., C. W. Schaefer & T. M. Withers (eds.), Biology, ecology, and evolution of gall-inducing arthropods. Science Publishers, Enfield, New Hampshire, USA.
RAMAN, A. 1994. Adaptational integration between gall-inducing insects and their host plants, pp. 249–275. *In* Ananthakrishnan, T. N. (ed.), Functional dynamics of phytophagous insects. Science Publishers, Lebanon, New Hampshire, USA.
ROBBINS, J. 1992. *Argyresthia retinella* Zell. (Lepidoptera: Yponomeutidae) a gall causer. Cecidology 7:53.
SHORTHOUSE, J. D. & O. ROHFRITSCH (EDS.). 1992. Biology of insect-induced galls. Oxford University Press, New York.
SOKAL, R. R. & F. J. ROHLF. 1981. Biometry. 2nd ed. Freeman, New York, USA.
ŠPATENKA, K., O. GORBUNOV, Z. LAŠTUVKA, I. TOŠEVSKI & Y. ARITA. 1999. Handbook of Palaearctic macrolepidoptera. Vol. 1. Sesiidae–Clearwing moths. Gem, Wallingford, England.
SPOONER, B. M. & J. P. Bowdrey. 1995. Checklist of British galls and gall-causing organisms. 1. Lepidoptera: preliminary list. Cecidology 10:84–100.
SYSTAT. 1992. Statistics version 5.2 ed. SYSTAT Inc.
TAUBER, M. J., C. A. TAUBER & S. MASAKI. 1986. Seasonal adaptations of insects. Oxford, New York.

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